Current Water Deficit Stress Simulations in Selected Agricultural System Models

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Abstract

System models that adequately simulate plant water stress effects are valuable tools for developing management practices that help improve water-use efficiency in agriculture. Plants experience water stress when water supply in the soil fails to meet the demand. Although it is easy to define the concept, accurate quantification and representation of water stress in crop models have been a challenge in system modeling. A critical review of literature shows that the water deficit stress modulates: (i) phasic plant developmental rates, (ii) leaf initiation and expansion growth, (iii) photosynthesis, (iv) carbon allocation and partitioning, and (v) root length and density in soil layers. In this paper, we present reviews of current simulations of plant water stress and its integration with crop growth and development processes in the APSIM, CropSyst, DSSAT-CSM, GLYCIM, and RZWQM models. In general, these models use the ratio of actual to potential transpiration or evapotranspiration to represent water stress. Potential evapotranspiration in general is computed by Penman–Monteith or Priestley–Taylor equations treating plant canopy as a big-leaf. In plants, the processes of carbon assimilation, transpiration, energy balance, and stomatal behavior are coupled. In the above models, there are no explicit simulations of leaf energy balance and leaf temperature or stomatal conductance in quantifying transpiration and photosynthesis. For improved simulations of crop growth and development under water deficit conditions, accurate simulations of these coupled processes governing water movement through the soil-plant-atmosphere continuum is essential. In this article, we also reviewed and presented examples of models (those not included in the five models listed above) that address these coupled processes. Results of performance evaluations of the above models in specific water deficit experiments substantiate their potential in developing cost-effective and scientifically sound decision support tools in agricultural water management.

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Water is fundamental for the normal physiological activities and membrane transport processes in plants and, as such, is the most limiting factor in agriculture. Water deficit stress (hereafter referred to as "water stress") refers to a condition in which plant cells and tissues have less than full turgor because of transpiration demand in excess of root water uptake, adversely affecting the growth and development processes and thus potentially limiting productivity. Increasing demand for agricultural products for food, fodder, and fuel with increasing human population calls for more efficient use of water in the agricultural sector in the future. In this context, there is an increasing challenge for scientists to develop innovative soil-water-nutrient-crop management practices that are more water-use efficient and sustainable. During the past decades, reductionist approaches led to a better understanding of the functional processes of the various components of the agricultural system and their roles in carbon gain vs. water loss (water-use efficiency—WUE). To address the evolving challenges of the 21st century agriculture, especially in the arena for increasing WUE of cultivated crops, whole system based studies synthesizing and integrating knowledge from their various components are needed. In this direction, agricultural system models are effective tools for integration and synthesis of knowledge gained from component experiments (Ahuja et al., 2007). These models allow the study of the behavior of the agricultural system in response to management of water and other natural resources.

Accurate simulations of water stress and its effects on various plant growth and development processes are critical for the successful applications of agricultural system models in field research and technology transfer for improving WUE. The objective of this article is to review and present the simulation procedures for water stress quantification and its integration with various crop growth and development processes in the APSIM, CropSyst, DSSAT-CSM, GLYCIM, and RZWQM models. A brief review of the current knowledge of the plant growth responses to water stress and interactions is also presented. We conclude the paper with examples of model testing, validation, and applications in specific water stress experiments conducted in the past.

Quantitative Measures of Water Stress

Plant water stress affects turgidity, cell enlargement, photosynthesis, respiration, and many other physiological processes in the plant. Verasan and Phillips (1978) proposed the use of cumulative plant evapotranspiration or transpiration as a better integrator of the effects of water stress on various plant physiological processes than soil-water potential. Plant evapotranspiration or transpiration is intimately coupled with stomatal conductance, CO_2 exchange, and a number of other interacting environmental and biological processes. Stomatal conductance (the diffusive conductance of leaf surfaces to water vapor) is the key element in the system that can modify all other processes. However, it may vary over a wide dynamic range and is affected by solar irradiance, humidity of the air, CO_2 partial pressure of the air, leaf temperature, and plant water stress. Stomatal conductance varies within and among leaves and among layers in a canopy. To facilitate accurate representation of water stress affects on the various components of the agricultural production system, an ideal system model needs to simulate all these components and processes in adequate detail. In this regard, current cropping system models need a great deal of improvement with respect to the effect of water stress on plant processes—particularly transpiration, photosynthesis, carbon allocation, canopy temperature, and the resulting water-use efficiency for production (Ahuja et al., 2006). Most current crop models use a simple stress factor approach to quantify this effect. In some models, a daily crop water stress is calculated as $1 - AT/PT$, where AT is the daily actual water uptake and PT is daily potential transpiration (Hanson, 2000; Sudar et al., 1981). Dale and Daniels (1995), on the other hand, used ET/PET to quantify water stress, where ET and PET are actual and potential evapotranspiration. Morgan et al. (1980) used the ratio of actual available soil moisture to available soil moisture at field capacity in the soil profile as an indicator of soil-moisture stress. In the case of a shallow water table, crop wet stress (water stress under wet conditions) was quantified by summation of days when the water table is within the top 30 cm of the soil profile (Ahmad et al., 1992; Evans et al., 1991). In this section, we present a review of approaches to simulate of soil-water stress in the APSIM, CropSyst, DSSAT-SCM, GLYCIM, and RZWQM models. In general, in all the above models, a stress factor is calculated that varies between 0.00 and 1.00.

APSIM v 5.0 Generic Plant Module

Four water deficit factors are calculated which correspond to four plant processes each having different sensitivity to water stress, i.e., photosynthesis, phenology, leaf-expansion, and nitrogen fixation (www.apsru.gov.au/apsru; verified 27 May 2008).
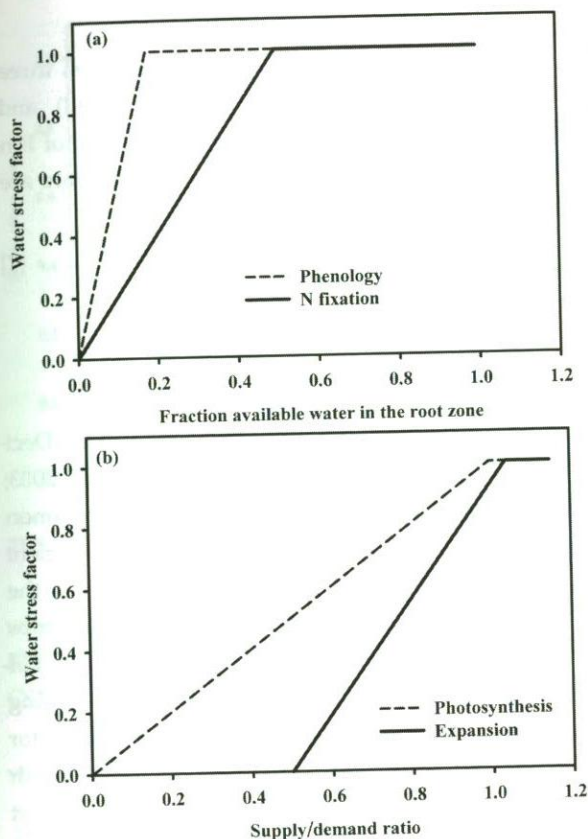
Fig. 1–1. Relationship between stress factors for N fixation and phenological development (a) and photosynthesis and leaf expansion to the ratio of supply to demand for soil water (b) in the APSIM generic plant module. A factor of 0 is complete stress and 1 no stress (www.apsru.gov.au/apsru; verified 27 May 2008).

In the generic plant module, a soil-water availability ratio or fraction available water in the root zone (SWAR) is calculated as:

$$SWAR = \frac{(sw - ll)}{(dul - ll)} \qquad [1]$$

sw is volumetric soil-water content, ll is the lower limit of soil-water holding capacity, and dul is the drained upper limit of soil-water holding capacity. This ratio is used in the relationships illustrated in Fig. 1–1a to derive stress factors for nitrogen fixation and phenological development. A factor of 0 is complete stress and 1 no stress. Likewise, Fig. 1–1b shows the relationship between the stress factors for photosynthesis and leaf expansion growth and the ratio of supply to demand for soil water.

The soil-water balance module in APSIM was adapted from the DSSAT models. As such, there are no coupled simulations of plant transpiration with the processes of carbon assimilation, energy balance, and stomatal behavior.

CropSyst

In CropSyst (Stöckle et al., 2003), crop growth is modeled to depend on three factors: transpiration (water limited), carbon fixation (radiation-limited), and nitrogen uptake (nitrogen- limited). Each one of these factors is capable of limiting growth. Water limited biomass growth (B_T) and developmental rate are affected by calculating a water stress factor (SWSF) defined as:

$$SWSF = \frac{AT}{PT} \qquad [2]$$

AT is the actual transpiration and PT is the potential transpiration.

DSSAT Cropping System Model (DSSAT-CSM)

The Cropping System Model (CSM) is the core crop simulation model of the Decision Support System for Agrotechnology Transfer (DSSAT) (Jones et al., 2003; Hoogenboom et al., 2004). The soil-water balance is simulated with a common water balance on the basis of Ritchie (1998), while crop growth and development are simulated with individual crop modules that encompass CROPGRO for the grain legumes and CERES for the grain cereals, as well as modules for other crops (Boote et al., 1998; Ritchie et al., 1998; Singh et al., 1998). The daily soil-water balance in all the DSSAT models uses the Ritchie (1985) one-dimensional "tipping bucket" approach, which simulates soil-water flow and root water uptake for each individual soil layer. Potential root water uptake is a function of root length density, rooting depth, and root distribution and the actual soil-water content for the layers where roots are present. Potential evapotranspiration can be calculated by either Priestley-Taylor (Priestley and Taylor, 1972; Ritchie, 1972; 1985) or Penman-Montieth-FAO56 (Allen et al., 1998) approach. Potential transpiration is a function of the leaf area index and potential evapotranspiration.

The same methodology is used for the actual calculation of the water stress or drought factors because of the common water balance among all crop modules, while the implementation and impact might differ, depending on the crop module. The basic principle for determining water stress is the comparison between potential transpiration or demand and potential root water uptake or plant extractable soil water. Under well-watered conditions, potential root water uptake is higher than potential transpiration. As the soil dries out because of root water uptake, potential root water uptake decreases. At a certain stage, a threshold is reached where the first water stress or turgor factor, called TURFAC(SWDF2), is activated (Fig. 1–2). This level of water stress is mainly implemented to modulate expansive growth, which in many cases is more sensitive to drought stress than the other growth and development processes.
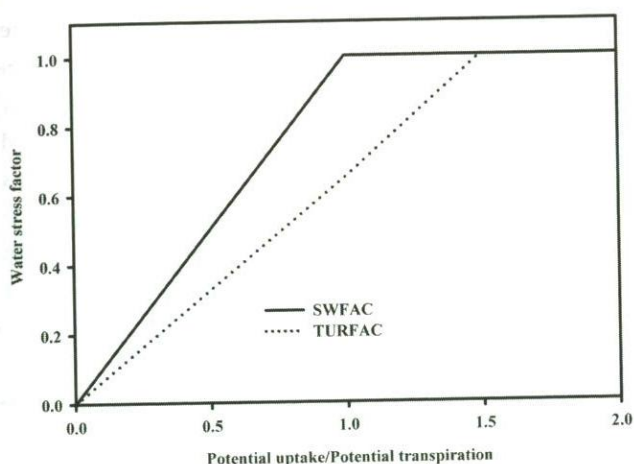
Fig. 1–2. Relationship used to calculate soil-water stress factors, SWFAC(SWDF1), and TURFAC(SWDF2) in DSSAT-CSM models (Ritchie, 1998).

$$TURFAC = \frac{TRWUP}{RWUEP1*EPo} \qquad [3]$$

where TRWUP is potential root water uptake and EPo the potential transpiration. RWUEP1 is a species-specific parameter that is currently set to 1.5 for all DSSAT-CSM crops.

When potential transpirational demand equals or exceeds the potential root water uptake, a second stress factor, called SWFAC(SWDF1), is activated (Fig. 1–2):

$$SWFAC = \frac{TRWUP}{EPo} \qquad [4]$$

SWFAC mainly affects growth and biomass related processes as well as phenology. For certain crops, a drought stress might actually increase the development rate and reduce the number of days to flowering, seed set, or physiological maturity, while it might decrease the development rate for other crops. Under nonstress conditions, both factors are set to 1. Once the stress factors have been activated, they decrease to a value less than 1 proportionally to the severity of the difference between potential transpirational demand and potential extractable soil moisture (Fig. 1–2). In the model, both stress factors are used either as a direct multiplier on a growth or development rate that ranges from 1 for no stress to 0 for complete stress or indirectly as a lookup function that affects growth or development.

GLYCIM

The soybean [*Glycine max* (L.) Merr.] simulation model GLYCIM, initially developed by Acock et al. (1985), is mechanistic and operates at the physical and physiological process level. Water stress in GLYCIM can affect both stomatal resis-

tance and the percentage of time the plant organs expand. A stomatal closure factor (SCF) is calculated from the ratio of available water weighted by root density. Stomata are totally closed (SCF = 0.1) if the leaf water potential drops below a threshold. Additional carbon is diverted from vegetative growth and supplied to root growth depending on the degree of water stress. The water stress effects on growth rate are based on leaf turgor pressure and the ability to osmoregulate. GLYCIM calculates leaf turgor pressure at hourly time steps and adjusts growth rate for water stress. During growth, the threshold turgor pressure required for cell growth adjusts dynamically. Next, the relationship between leaf water potential and leaf turgor pressure is controlled by osmoregulation. GLYCIM calculates the potential for water stress and its effect on growth rates in the following possible scenarios.

1. No water stress: Potential transpiration rate is such that the demand for water uptake can be met without shoot water potential falling to the point where the shoot loses turgor and stops growing.

2. Mild water stress with some growth adjustment: Potential transpiration rate is such that the demand for water uptake cannot be met without shoot water potential falling to the point where the shoot loses turgor and stops growing for part of the period. When this happens, additional carbon is partitioned to the roots for new growth. Since new roots have a lower resistance than older roots, this allows an increase in water uptake (Acock et al., 1985).

3. Moderate water stress: At higher transpiration demands, both leaf water potential and leaf turgor pressure decrease. Up to a point these adjustments may allow the plant to take up enough water to maintain low stomatal resistance. When leaf turgor pressure reaches a critical point (between 0.50 and 0.20 MPa), the stomata close. Leaf water potential is calculated iteratively. The proportion of time the plant grows (SGLI) is calculated as the ratio between the difference between leaf water potential of the current time step and turgor pressure and the leaf water potential at the previous time step and turgor pressure. This proportion (SGLI) is also applied to reduce the maximum amount of carbon used in growth.

4. Severe moisture stress: When leaf turgor pressure falls below 0.20 MPa then the stomata begin to close and all above ground plant growth stops.

In the evening when ET rates are low again, typically in the evening hours, the plant can recover some growth as the leaves rehydrate.

Root Zone Water Quality Model (RZWQM)

A water fitness factor (E_w) is calculated to represent the water stress experienced by the crop, defined as the ratio between the actual and potential transpiration rates of the crop, respectively). It is bound within the generic plant model such that $0.15 \leq Ew \leq 1.0$

$$Ew = 0.15 + 0.85\frac{AT}{PT}$$ [5]

where AT is the daily actual water uptake and PT is the daily potential transpiration.

In RZWQM, water entering into the system at the soil surface is subjected to evapotranspiration losses from a partially covered soil, further partitions of evaporation into the bare soil and residue covered fractions are affected using the extended Shuttleworth and Wallace (1985) ET model (Farahani and DeCoursey, 2000). There are no coupled simulations of plant transpiration with the processes of carbon assimilation, energy balance, and stomatal behavior.

Effects of Water Stress on Plant Growth and Development

Phenology

Experimental Evidence

Angus and Moncur (1977) found hastened development in wheat (*Triticum aestivum* L.) plants after mild soil-water stress and delayed development after severe stress, the later likely associated to apex development cessation during severe stress. The hastening development due to mild water stress was more difficult to explain; one suggestion was that the increased leaf temperature, which accompanied water stress, hastened development similar to that of an increase in ambient temperature. Another possibility was the plant acclimation to the stress modifying the normal sequences of development. Water stress shortened the life-span and flowering period of five Namaqualand ephemeral species sown in the months of April, May, June, and July (Steyn et al., 1996). The water stressed plants were smaller, with relatively fewer inflorescences and a shorter flowering period than plants grown with sufficient water.

Link et al. (1990) observed delay by about 10 d in phenological development and leaf senescence in cheatgrass (*Bromus tectorum* L.) maintained at low negative water potentials through irrigation. Water stress delays flowering and maturity in both maize, *Zea mays* L., and sorghum, *Sorghum bicolor* (L.) Moench, (Farre and Faci, 2006). In maize, water deficit (mild or severe) delayed leaf appearance by 6 d depending on leaf number and tasseling up to 3 d (Traore et al., 2000). NeSmith and Ritchie (1992) and Abrecht and Carberry (1993) observed delayed leaf tip emergence, tassel emergence, silking, and onset of grain filling in maize subjected to varying amounts of water stress. Soil-moisture stress imposed at different stages of growth in maize produced contrasting effects on its development and yield. Water deficit during the reproductive period (after tasseling) can

increase the interval from silking to pollen shed (Herrero and Johnson, 1981) and shorten the grain-filling period (Westgate, 1994). Water deficit before tasseling delayed silking but not tasseling resulting in grain yield loss (Kefale and Rana-mukhaarachchi, 2004). Cakir (2004) observed 66 to 93% yield losses because of extended water stress during tasseling and ear formation stages and highest yields in fully irrigated treatments but for water stress only during the vegeta-tive growth stage.

In soybean, water stress has been shown to hasten the onset of reproduc-tive stages while the appearance of nodes is delayed, resulting in fewer nodes (Desclaux and Roumet, 1996). Physiological maturity of soybean is consistently accelerated by water stress during grain filling, which Ruiz-Nogueira et al. (2001) modeled by allowing developmental rate to accelerate with plant water stress. The appearance of flowers and pods is also faster under water stress resulting in shorter durations of growing time and lower seed weights (Lawn, 1982; Desclaux and Roumet, 1996). Soybean can also survive periods of stress since it can put on new flowers when water stress is relieved (Lawn, 1982).

Variable effects of water stress on plant development have been reported in the literature for different crops. Effect of water stress on plant development can be highly specific to the species and within species the stress affects differently depending on its timing in relation to the growth stages. Angus and Moncur (1977) recommend that, though of less importance than the influences of tempera-ture and photoperiod, water stress still affect phasic development of field crops to modify the developmental stages on the order of a few days and hence must be included in crop developmental models for predictions within an accuracy of a few days. Crop models that simulate the effects of water stress on crop phenology need to take into account the above facts when modeling different crop species.

Modeling Approaches

APSIM v 5.0 Generic Plant Module

Phasic development of the crops is modulated by water stress e.g.: Between the stages of emergence and flowering, the calculated daily thermal time is reduced by water and nitrogen stresses, resulting in delayed phenology when the plant is under stress.

Simulations of water stress effects on the growth and development in the maize crop module is similar to the generic plant growth module described above. However, in the maize growth module, simulation of the effect of water and N stresses in delaying time to silking is also affected.

CropSyst

In CropSyst, simulation of crop phenology is based on thermal time. Accumulated thermal time required for particular stages of growth are decreased by water stress. This is based on the assumption that plants will be warmer if transpiration is limited by water stress and will accelerate development. The correction is implemented by adding temperature to the T_{max} input to the plant temperature equation according to the following equation:

$$T'_{max} = T_{max} [1 + (1.5 \ VPD_{max}) (1 - SWSF) \ PSWS] \qquad [6]$$

where T_{max} is the daily maximum air temperature, VPD_{max} is the daily maximum vapor pressure deficit [based on actual and saturated vapor pressure (VP_{sat}) at T_{max}] limited to a range of 0 to 6 kPa, SWSF is the daily plant water stress index, and PSWS is the phenologic sensitivity to water stress, a_crop input parameter. For crops whose development is not expected to be affected by water stress, this correction can be deselected by the user (PSWS = 0).

DSSAT-CSM

Water stress interactions with crop phenological development are not simulated in the CERES crop modules. However, in CROPGRO, the stress factor SWDF1 is used to influence progression of reproductive stages (delays progress to beginning pod and seed but accelerates progress from beginning seed to physiological maturity), and it uses SWDF2 to reduce rate of leaf appearance (V-stage), reduce internode elongation (affects height and width), shift assimilate from shoot to root, and shift assimilate allocation from stem to leaf (function of a cumulative turgor stress).

GLYCIM

In GLYCIM, no direct adjustments are made to phenological development under water stress. The stomatal closure factor is used to decrease pod and seed weight. Relative growth and appearance rates of the various organs are dependent on carbon supply. As water stress reduces carbon supply, relative growth and development rates will change depending on carbon availability.

RZWQM

In the generic plant growth module of RZWQM, severe water stress ($Ew < 0.6$, Eq. [5]) delays and moderate stress ($Ew > 0.6$, Eq. [5]) hastens plant development irrespective of the simulated species and its growth stages. In the model, growth stage is a theoretical index of plant development and ranges from 0 (seeds) to 1 (totally mature plant). Growth stage (GS) is defined as the stage reached by the dominant age class at the development rate for the dominant age class modified by the current environmental fitness (Ev)

$$GS = \sum_{j=1}^{t} DjEv$$

[7]

where, Dj (rate) is the inverse of the minimum time required to pass through the current average phenological stage under optimum environmental conditions. Ev is the environmental fitness at time j. Environmental fitness estimates the suitability of the environment for plant growth. Fitness at time j (Ev) is determined as the product of the current temperature fitness (Et), and the minimum of the current water (Ew) and nutrient fitness (En),

$Ev = Et * Em$

[8]

where, Em is the minimum of Ew and En. All stress factors are scaled between 0 and 1. Detailed procedures for computations of Et, En, and Ew are described elsewhere (Hanson, 2000).

Photosynthesis and Biomass Production

Experimental Evidence

Plant response to water stress can potentially involve mechanisms that tend to limit water consumption; stomatal closure is the most conspicuous of these mechanisms, which result in reduction of both transpiration and photosynthesis. Stomatal responses to root signals from desiccating soils have been identified (Gowing et al., 1990; Davies and Zhang, 1991; Passioura, 1988; Steudle, 2000). Stomatal control affecting gas exchange is an early plant response to soil-water deficits (Cornic and Massacci, 1996). In a 1-yr study with pearl millet [*Pennisetum glaucum* (L.) R. Br.], the dominant role of stomata in reducing crop water use under preanthesis water stress and negligible role under postanthesis water stress were reported (Winkel et al., 2001). Boyer (1970) reported inhibition in the rates of photosynthesis in field grown maize whenever leaf water potentials dropped below −0.35 MPa, whereas soybean was found to be unaffected by desiccation until leaf water potentials were below −1.1 MPa. Field crops respond to slowly developing mild water deficits by stomatal closure in response to the migration of chemical compounds (including abscisic acid, ABA) synthesized in desiccating root segments (Chaves et al., 2002). When drought is prolonged, this is followed by a downregulation of photosynthesis to match (eliminate) the decline in intercellular CO_2 following stomatal closure. In response to soil-water deficits, in addition to stomatal inhibition, nonstomatal inhibition of photosynthesis can also occur in plants (Bunce, 1988). In sugarcane (*Saccharum* sp.), mild water stress induced decline in photosynthesis was caused by stomatal closure and the biochemical processes of sucrose and starch synthesis (Du et al., 1998). As water stress inten-

sifies, the photosynthetic metabolism is progressively downregulated in plants (Flexas et al., 2004).

Several studies in the past showed that the greatest reduction in grain production in maize is caused by moisture stress imposed at the silking–pollination stage (Denmead and Shaw, 1960; Grant et al., 1989). In container-grown corn, soil-water deficit before silking reduced grain yield by 25%, at silking by 50%, and after silking by 21% (Denmead and Shaw, 1960). Water stress before tasseling and flowering can cause a severe yield reduction because of poor pollination that is affected by a delay in silking with respect to pollen-shedding in maize (Hall et al., 1981).

Modeling Approaches

APSIM v 5.0 Generic Plant Module

Each day, two estimates of the daily biomass production are calculated, one limited by available water for transpiration (DM_T) (Eq. [9]), and the other limited by radiant energy (DM_R) (Eq. [10]). The minimum of these two estimates is the actual biomass production for the day as:

$$DM_T = SW * TE \qquad\qquad [9]$$

where, SW is available soil-water uptake (mass), and TE is the transpiration efficiency derived from the transpiration efficiency coefficient and the vapor pressure deficit estimated from daily temperatures.

$$DM_R = rue * Ri \qquad\qquad [10]$$

where, rue is radiation-use efficiency, and Ri is the intercepted total solar radiation. The rue incorporates temperature, oxygen deficit [water logging], and nitrogen stresses. The value of rue is not limited by temperature over a range between the first and second optima. Temperatures outside this range reduce rue to zero at a base and maximum temperature. The rue is linearly interpolated between the phenological stages specified in a table. Biomass calculated by the above methods is modified by the water deficit factor for photosynthesis (Fig. 1–1b). There are no coupled simulation of plant transpiration with the processes of carbon assimilation, energy balance, and stomatal behavior.

CropSyst

In CropSyst (Stöckle et al., 2003), crop growth is modeled to depend on three factors: transpiration (water limited), carbon fixation (radiation-limited), and nitrogen uptake (nitrogen- limited). Each one of these factors is capable of limiting growth.

Water-limited growth (Gw) follows the approach suggested by Tanner and Sinclair (1983):

$$Gw = \frac{K\ Ta}{VPD} \qquad\qquad [11]$$

where Gw is crop potential transpiration dependent biomass production in kg m^{-2} day, Ta is crop actual transpiration (kg m^{-2} day), K is the aboveground biomass/water transpired ratio (kPa), and VPD is the daytime mean vapor pressure deficit (kPa).

When VPD is too small, Eq. [11] can grossly overestimate biomass production. A second biomass growth estimate is calculated, and the minimum of the two is selected. This second estimate is calculated following Monteith (1977) as:

$$BIPAR = rue * IPAR \qquad\qquad [12]$$

where BIPAR is the intercepted photosynthetically active radiation dependent biomass production (kg m^{-2} d^{-1}), rue is the radiation-use efficiency (kg MJ^{-1}), and IPAR is the daily amount of crop-intercepted photosynthetically active radiation (MJ m^{-2} d^{-1}).

The crop water uptake or water limited actual crop transpiration (T_A) is calculated as the product of the water potential difference between the soil and the crop canopy and crop hydraulic conductance (Stöckle and Jara, 1998) under specified evaporative demand (potential transpiration) and stomatal behavior, allowing the calculation of the water stress factor (SWSF) in Eq. [2], water-limited biomass growth (B_T) is then affected by the water stress factor

$$B_T = SWSF * Gw \qquad\qquad [13]$$

where Gw and B_T are in kg m^{-2} d^{-1}.

This approach accounts indirectly for the coupling of plant transpiration with the processes of carbon assimilation, energy balance, and stomatal behavior.

DSSAT-CSM

In the CERES and CROPGRO crop modules, the stress factor, SWDF1, decreases net biomass production of the day in direct proportion. However, solar radiation drives net biomass production and N stress is also a limiting factor.

GLYCIM

GLYCIM uses single-leaf photosynthetic characteristics to calculate crop canopy characteristics and canopy gross photosynthetic rate and scales this to the plant. Carbon assimilation is modeled by a hyperbolic equation that is a function of CO_2 and temperature. Photorespiration rate and maintenance respiration rate are calculated and subtracted to get net photosynthetic rate, which is corrected for stomata closure caused by water stress. The net carbon fixation rate and the

rate of carbon translocation out of the leaves are also calculated. The stomatal closure factor is used to reduce the net photosynthetic rate. The factor that is used to reduce shoot growth time is also used to reduce the potential carbon available for growth and the maximum amount of carbon needed to grow the plant at its potential rate. In this way, carbon availability can limit growth in the case of water stress. Notwithstanding, there are no coupled simulations of plant transpiration with the processes of carbon assimilation, energy balance, and stomatal behavior.

Carbon availability affects the expansion and dry weight gain of all the organs on the plant. Root growth influences water uptake, plant water relations, and stomatal conductance. Since the model was originally designed to examine the interactions between CO_2 and other environmental factors, all the processes in the model have been brought to approximately similar level of mechanistic detail.

RZWQM
Current day biomass growth (BMp) is modified by the minimum of water and N stress.

$$BM = BMp * Min. (Ew,En) \hspace{3cm} [14]$$

where BM is the net biomass fixed per day, and Ew is the water and En the nitrogen stresses.

Carbon Allocation and Partitioning

Experimental Evidence
Assimilate partitioning in plants is governed by the processes of carbon assimilation, translocation, respiration, metabolic rates, storage, external environmental conditions, etc., acting over a wide range of time scales. Inadequate information on the mechanisms governing assimilate allocation and portioning is one of the main limitations to the development of process-based models of whole plants (Dewar, 1993). Changes in carbon partitioning between leaf metabolites and in carbon allocation and distribution between different organs allows plants to adapt to water shortage. One such adaptation is reflected in the increased root–shoot ratio consequent to reduced leaf elongation growth and a decrease in grain set and development rates (Chaves et al., 2002). Plant survival under combined effects of all environmental stresses acting on it depends on the integrated response at the whole plant level in carbon assimilation and allocation to different organs and retaining the reproductive ability (Pereira and Chaves, 1993). According to Passioura (1994), over the long term, modulation of leaf area, shoot–root partitioning, and root density may be of greater importance to plant water status. In kiwifruit

(*Actinidia chinensis* Planchon) under high water stress, the root-to-shoot ratio was 3.5 times higher than nonstressed plants, showing that water stress alters the pattern of dry matter distribution favoring the roots (Chartzoulakis et al., 1993). In the context of a plant growth model, the importance of modeling the key adaptations to water stress such as osmoregulation, modulation of leaf area, shoot–root ratio, and root density has been identified (Thornley, 1996). Water is an important determinant of the allocation of assimilate between roots and shoots during crop growth (Chen and Reynolds, 1997). Water stress affects biomass accumulation via limiting photosynthesis and leaf expansion and affects biomass allocation and partitioning to different growing parts (Saini and Lalonde, 1998).

Modeling Approaches

APSIM v 5.0 Generic Plant Module

In APSIM, modifications of assimilate partitioning by water stress is not simulated explicitly (www.apsru.gov.au/apsru; verified 27 May 2008).

CropSyst

In CropSyst, canopy expansion is stopped at large values of AT/PT (about 0.9 or so, which is user defined), while root expansion can tolerate a lower ratio, effectively changing the partitioning of carbon between aboveground and root fractions. Thus, root penetration is not reduced until significant stress has developed.

Grain yield simulation depends on total biomass accumulated at physiological maturity (B_{PM}) and the harvest index (HI = /harvestable yield/aboveground biomass) (Stöckle et al., 2003):

$$Y = B_{PM} * HI \qquad [15]$$

where Y is grain yield (kg m^{-2}) and B_{PM} biomass at physical maturity (kg m^{-2}).

The harvest index is determined using as base an unstressed harvest index modified according to stress intensity (water and nitrogen) and crop sensitivity to stress during flowering and grain filling. Harvest index for a nonstressed crop is reduced depending on the severity of water stress around flowering (sink reduction) and the crop sensitivity to stress during flowering. Stress during grain filling also can reduce the harvest index, depending on C translocation ability of the crop or cultivar.

DSSAT-CSM

Both CERES and CROPGRO crop modules of DSSAT shift partitioning to roots under water deficit. The CROPGRO code, for example, uses the following expression to modify partitioning to root.

$$FRRT = FRRT + ATOP * (1.0 - fs) * (1.0 - FRRT) \qquad [16]$$

where ATOP is maximum fraction change in partitioning from top growth to roots if severe water or nitrogen stresses occur, fs is the minimum of the SWDF1 and NSTRES stress factors, NSTRES is the nitrogen stress factor (1 = no stress, 0 = max stress), and FRRT is the fraction of vegetative tissue growth that goes to roots on a day (g[root]/g[veg]).

Both crop modules (CROPGRO and CERES) are different in allowing water deficit effects on single grain growth. CERES-maize allows SWDF1 to directly reduce grain growth rate. CROPGRO does not reduce grain growth rate directly with water deficit, but it does via water deficit effects on photosynthesis.

GLYCIM

In GLYCIM in response to water stress, the following modifications take place in carbon allocation and partitioning.

Mild water stress allocates additional carbon to the roots for new growth. Further increase in water stress reduces the maximum amount of carbon used in growth, and severe water stress stops all above ground plant growth. The potential growth rate of the above ground portion of the plant and total carbon available for growth are also reduced depending on the level of stress. This may affect partitioning depending on the relative amounts available for growth of the different organs.

RZWQM

In RZWQM, root shoot partitioning is affected by water and nitrogen fitness factors (stress) from germinated plants until reproductive stages. The following equations are used:

$$C_{ROOT} = C_{TOT} - C_{SHOOT}$$ [17]

$$C_{SHOOT} = C_{TOT}/[1.0 + (R_E/E_{WN})]$$ [18]

where C_{ROOT} is carbon partitioned to root, C_{TOT} is total carbon assimilated, C_{SHOOT} is carbon partitioned to shoot, R_E is root to shoot ratio at emergence, and E_{WN} is the maximum value among 0.5 and minimum value between Ew and E_N (Ew is the water fitness factor and E_N is the nitrogen fitness factor).

The model also calculates water-stress induced shoot death and loss of plant population from germination to reproductive stages.

Leaf Expansion

Experimental Evidence

In leaves, stomata respond either to a change in leaf turgor or cell water potential or to water vapor pressure deficit between the leaf and the atmosphere (Ludlow, 1980; Maroco et al., 1997). In maize cultivars, soil-water deficit reduced both leaf

area and dry matter accumulation; however, the leaf expansion rate was observed to be more sensitive to low turgor, and the expansion ceased when turgor reached 0.2 MPa (Sobrado, 1986). Many studies provided evidence that led to a conclusion that stomatal responses in water stressed plants are more linked to soil-moisture content than to leaf water contents. This led to the hypothesis that in addition to hydraulic signals, stomata are responding to chemical signals like ABA that are synthesized in roots exposed to desiccating soil (Davies and Zhang, 1991; Davies et al., 2000). Chemical signals from the roots were found to modulate cell expansion rate more than net carbon assimilation and translocation rates (Turner and Begg, 1981; McCoy et al., 1990). Leaf expansion growth was considerably reduced by mild soil-water deficits that do not affect photosynthesis, and this effect continued for several weeks after the plants had been rewatered (Tardieu et al., 1999, 2000; Granier and Tardieu, 1999; Lecoeur et al., 1995). While there is conclusive evidence on the synthesis and circulation of ABA in plants in response to soil-water deficit, and its role in the control of stomatal aperture and leaf expansion rates, less evidence exists on the mechanisms of long-distance transport of ABA from the roots to the leaves. Decrease in growth induced by water deficit was a consequence of a reduction in both photosynthesis and photosynthate partitioning that adversely affects leaf area development (Chartzoulakis et al., 1993). Water deficits, depending on the severity of the stress, reduce or terminate new leaf production in peach [*Prunus persica* (L.) Batsch] trees (Steinberg et al., 1990). However, conflicting experimental reports in the literature show that water stress affects new soybean leaf production in some cases (Takami et al., 1981) but not in others (Hoogenboom et al., 1987). Improved understanding and quantification of the biomass assimilation and partitioning processes in response to various levels of water stresses in specific crop species and cultivars would help in building plant models that respond to soil-water deficits better.

Modeling Approaches

APSIM v 5.0 Generic Plant Module

Potential leaf area index (LAI) is a product of leaf number, leaf size, number of plants per m^2, and the water stress factor for expansion growth.

There are four causes of leaf senescence: age, light competition, water stress, and frost. The plant senescence routines calculate a senesced LAI for each of these stresses each day and take the maximum of the four values as the day's total senescence.

A fraction of the oldest green leaf dies each day after flowering. This senescence due to age occurs at a rate of leaves per day. A rate of senescence of other

plant parts can also be specified (such as stems) in terms of a fraction of dry weight senesced for each fraction of canopy senesced.

Water stress during crop growth that causes leaf senescence is calculated as:

$$LAIsf = 0.05 * [1 - swdef(photo)] \qquad\qquad [19]$$

$$LAIs = LAI * LAIsf \qquad\qquad [20]$$

where LAIsf is the factor for calculation of senesced LAI, LAIs is the portion of LAI senesced, and swdef(photo) is the soil-water deficit factor for photosynthesis.

A fraction of plants (0.044) will be killed each day because of water stress once the cumulative water stress factor for photosynthesis exceeds 4.6.

If the crop has not germinated within 40 d of sowing because of lack of germinating moisture, all plants are killed.

If the cumulative phenological water stress factor exceeds 25, all plants are killed because of water stress prolonging phenology.

CropSyst

In CropSyst, the increase of leaf area during the vegetative period, expressed as LAI, is calculated as a function of biomass accumulation, specific leaf area, and a partitioning coefficient. Leaf area expansion is affected directly by water stress in addition to its indirect effect through decreased growth rate. Leaf area duration, specified in terms of thermal time and modulated by water stress, determines canopy senescence.

DSSAT-CSM

In the CERES and CROPGRO modules, the stress factor TURFAC is used to modulate the simulated leaf area growth increment of the day. Use of 1.5 in the calculation of this factor (Eq. [3]) facilitates the expansion process of the day to decrease earlier with water deficit, than does dry matter growth (Fig. 1–2). CROPGRO also reduces height increase (internode length) and width increase with the SWDF2 factor.

GLYCIM

In GLYCIM, as discussed above, with higher transpiration demand (moderately severe water stress), both leaf water potential and leaf turgor pressure decrease. Up to a point these adjustments may allow the plant to take up enough water to maintain low stomatal resistance. Stomata close when leaf turgor pressure reaches a critical point (between 0.50 and 0.20 MPa). Leaf water potential is calculated iteratively. The proportion of time the plant grows (SGLI) is calculated as the ratio between the difference between leaf water potential of the current time step and turgor pressure and the leaf water potential at the previous time step and turgor pressure. This proportion (SGLI) is also applied to reduce the

maximum amount of carbon used in growth. When leaf turgor pressure falls below 0.20 MPa (severe moisture stress), the stomata begin to close and all above ground plant growth stops. In the evening when ET rates are low, the plant can recover some growth as the leaves rehydrate.

RZWQM

Direct effects of water stress on leaf growth are not modeled in the generic crop growth module of RZWQM.

Root Growth

Experimental Evidence

Efficient water and nutrient recovery of crops are greatly influenced by the rooting characteristics of the plant. Early responses of plants to water stress help survival through acclimation depending on improved functioning through alterations in gene expression to change metabolic and structural capabilities (Bohnert and Sheveleva, 1998). Acclimation changes resulting in increased root growth relative to shoot and temporary storage of assimilate in the stem are some of the early acclimation changes (Hsiao and Xu, 2000; Rodrígues et al., 1995). Water stress in maize increased root weight and decreased shoot weight, but after recovery a net mobilization of assimilates from roots to shoot was observed (Aggarwal and Sinha, 1983). Osmotic adjustment for maintaining cell-water potential was found to be a mechanism responsible for sustained root growth under water deficit conditions in maize (Saab et al., 1992; Hsiao and Xu, 2000).

Crops vary in rooting response to plant-water stress and irrigation strategy. Robertson et al. (1980) conducted field experiments to study the effects of water stress and irrigation levels on root distribution in maize, soybean, and peanut (*Arachis hypogaea* L.). They observed no effect of water management on peanut and soybean root growth (root length per unit area to a depth of 150 cm), but the maize roots responded to irrigation with the largest root length increase observed in the light, infrequent irrigation treatment.

Modeling Approaches

APSIM v 5.0 Generic Plant Module

Increase in root depth between emergence and grain-filling stages is a daily rate multiplied by an exploration factor, a soil-water availability factor for the layer where the deepest roots are currently passing across, and a temperature factor. In severe water-deficit conditions, the root depth increase can be slowed down and even stopped by the function that incorporates the water stress factor for the day (similar to CERES-Maize model).

CropSyst

In CropSyst, canopy expansion is stopped with modest water stress (based on a user-defined threshold), while root penetration and proliferation can tolerate greater levels of stress so that more carbon is made available for root growth.

DSSAT-CSM

Both CROPGRO and CERES modules reduce the rate of root depth progression in a given layer as a function of water content of that layer (SWDFS), but CROPGRO accelerates root depth progression with plant water deficit (SWDF1) as well, making it a complex function.

CROPGRO calculates daily rooting depth as:

$$RTDEP = RTDEP + DTX\ RFAC2\ fx\ (SWDFS, SWEXF)\{1 + 0.25\ [1 - fy(SWDF1)]\}\ [21]$$

where fx is the minimum of SWDFS and SWEXF, SWDFS is equal to $[SW(L) - LL(L)]/\{0.25^*[DUL(L) - LL(L)]\}$ for layer for deepest roots, SWEXF is excess water-stress factor for layer with deepest roots (0–1), fy is the maximum of SWDF1 and 0.40, RTDEP is root depth (cm), DTX is thermal time that occurs in a real day on the basis of vegetative development temperature function (thermal days/day), and RFAC2 is root depth increase rate with time (cm/physiol. day). Equations for CERES are different because the fx function allows plant water deficit (SWDF1) along with SWDFS and SWEXF to restrict root depth progression, and they lack the acceleration with plant water deficit (SWDF1).

GLYCIM

In GLYCIM, with mild water stress, additional carbon is partitioned to the roots for new growth. Severe water stress reduces the maximum amount of carbon used in above ground growth. Finally, with severe moisture stress, all above ground plant growth stops. Root growth in the soil is additionally controlled by temperature, soil aeration, and soil strength. A favorability factor is calculated for each of these soil properties, and roots grow into the cells where the favorability factors are highest.

RZWQM

In RZWQM, daily biomass portioned for root growth is modified by the minimum of the water and nitrogen fitness factors (stress) (Eq. [17] and [18] above).

Interactions between Water and Nitrogen Stresses

Experimental Evidence

Plants in the natural environment characterized by varying environmental conditions over time and space are often subjected to multiple biotic and abiotic

stresses. In addition to the various plant growth and development processes discussed above, limitation in availability of water (water stress) seriously modifies plant root capacity to take in nutrients. In water-limited ecosystems, primary production is often modified by interacting effects of water and nitrogen availabilities (Mazzarino et al., 1998). Growth and accumulation of plant nutrients in maize is seriously affected by soil-water stress and evaporative demand (Verasan and Phillips, 1978). Evaporative water loss from the soil under a wheat crop was found to be significantly modified by the plant nitrogen status through modification of the canopy leaf area growth (Passioura, 2006). Compared with the independent effects, interacting water and nitrogen stresses resulted in significant reduction in grain yield, leaf longevity, and green leaf area index in maize (Wolfe et al. (1988a, 1988b). When water stress is a limiting factor, photosynthetic rate does not improve with nitrogen supply (Shangguan et al., 2000). In water and nitrogen stressed crop production systems, water-use efficiency and yield can increase with increased N, exemplifying an increasing degree of colimitation (Sadras, 2004).

In addition, symbiotic nitrogen fixation in legumes is seriously affected by soil drying, resulting in a reduced supply of N to the plant and lower yields (Sinclair et al., 1987; Sall and Sinclair, 1991; Purcell and King, 1996; Sinclair and Serraj, 1995).

Modeling Approaches

APSIM v 5.0 Generic Plant Module

In the generic plant module, grain N demand is driven by critical N content, but this demand is lowered if the plant is under N stress. Grain N demand is also affected by temperature (T) and water stress for expansion (SWAR) (Eq. [1]) using equations below.

$$NGTF = 0.69 + 0.125 * T \tag{22}$$

$$NGSWF = 1.125 - 0.125 * SWAR \tag{23}$$

where NGTF is the temperature factor and NGSWF is the modified water stress factor for expansion growth used for modifying nitrogen content in grain.

The greatest of these two factors is multiplied by the previously calculated N demand, i.e., if temperature is high or SWAR (expansion) is low (water stressed), the N demand will be increased above the level required to reach the critical N concentration. CERES-Maize uses very similar equations to shift grain N demand as a function of temperature and plant water stress.

The daily rate of potential nitrogen fixation is a function of the crop N fixing capacity (NFC), which varies with growth stage, crop biomass (i.e., the size of the crop), and soil-water stress.

$$NFC = NFR * BM * SWAR \text{ (fixation)} \tag{24}$$

where NFR is the nitrogen fixing rate, BM is the biomass, and SWAR (fixation) is the soil-water stress factor for symbiotic N fixation.

CropSyst

There are several instances of interaction between water and nitrogen stress in CropSyst. Plant nitrogen demand is constrained by water stress while nitrogen uptake is dependent on soil-water content and root proliferation (which can also be affected by water stress). If nitrogen stress limits growth in the presence of abundant water supply, water uptake will be limited by nitrogen limit on growth.

DSSAT-CSM

The N uptake functions in CROPGRO and CERES plant modules are dependent on the fraction available soil water of the given soil layer (SWDFS), with N uptake decreasing as soil-water content approaches the lower limit or the saturated upper limit. In addition, nodule growth and N fixation in CROPGRO are dependent on the plant water stress factor (N-fixation sensitivity uses a function between SWDF1 and SWDF2, depending on species sensitivity to water deficit). Use of soil-water status of the nodule zone to affect nodule growth and N fixation was attempted in early model versions but was discarded. In CROPGRO, the minimum of water and nitrogen stress is used for shifting partitioning to roots under water deficit (Eq. [16]). This stress interaction is not simulated in the CERES crop modules, although water deficit separately causes shift of assimilate to roots.

GLYCIM

GLYCIM simulates the soybean crop, which is a nitrogen fixer. Water–nitrogen stress interactions are not simulated. The nodules are affected by water stress only in terms of the effect of water stress on carbon availability. Water stress will therefore affect growth of nodules indirectly.

RZWQM

In RZWQM, growth stage is defined as the stage reached by the dominant class at the development rate for the dominant class reduced by the current environmental fitness E_v (Eq. [7]).

Ev is determined as the product of the current temperature fitness and the minimum of the current water and N fitness (Hanson, 2000).

Coupled Models of Stomatal Conductance, Photosynthesis, and Transpiration

Farquhar et al. (1980) pioneered in developing a comprehensive biochemical model of photosynthesis integrating all the essential processes affecting gas exchange at the suborganelle level in a C_3 plant leaf. However, application of the model for

carbon assimilation modeling at the leaf and canopy level is limited because of the many parameters that need to be quantified for scaling from the suborganelle level to canopy. Farquhar and von Caemmerer (1982) modified the model for extending its scope for applications in modeling photosynthesis at the leaf and canopy level. In nature, processes of stomatal conductance, transpiration, photosynthesis, respiration, and energy balance are coupled; modeling approaches should represent that coupling. Stomata control the leaf to air gas exchange in plants. Concise quantitative descriptions of stomatal behavior for development of coupled models of leaf energy balance, photosynthesis, and transpiration was lacking in literature, probably because of the daunting complexities involved in the processes.

Ball et al. (1987) described the stomatal behavior by a set of linear relationships that can aid in development of coupled models of CO_2, transpiration, and energy. Collatz et al. (1991) coupled the Farquhar and Caemmerer (1982) model of photosynthesis with Ball et al. (1987) model for stomatal conductance and energy balance to describe the physiological and environmental regulation of the gas exchange processes for a soybean canopy. Kirchbaum and Farquhar (1984) investigated temperature dependence of photosynthesis using the Farquhar et al. (1980) photosynthesis model. Grossman et al. (1995) linked the wheat model, DEMETER, to a soil–vegetation–atmosphere–transfer model that has coupled modules of energy balance of the canopy–soil, stomatal conductance, transpiration, and photosynthesis, which computes detailed evapotranspiration, canopy temperature, and the changing ratio of sensible to latent heat flux in response to elevated atmospheric CO_2 concentrations. Leuning (1995) and Wang and Leuning (1998) presented coupled models of stomata–photosynthesis–transpiration with multilayer canopy. Kirschbaum (1999) developed a forest growth model (CenW) coupling the carbon, energy, nutrient, and water cycles in the system. Tuzet et al. (2003) presented a model that couples stomatal conductance, photosynthesis, leaf energy balance, and plant water uptake in the soil–water–plant–atmosphere continuum. In this model, the Leuning (1995) stomatal model was modified by replacing the humidity deficit term by a function of leaf water potential and CO_2 concentration at the leaf surface by the intercellular CO_2 concentration. A complete coupling between stomatal conductance, flux of water through the plant and soil, and CO_2 exchange between leaves and atmosphere was achieved (Tuzet et al., 2003). Grant et al. (1999) developed detailed coupled stomatal conductance, photosynthesis, leaf energy balance, and plant water uptake models for simulating the effects of simultaneous changes of CO2 and water on wheat growth in FACE experiments. Kremer et al. (2008), in this volume, present a coupled model that was used by Stöckle et al. (2008), also in this volume, to evaluate simple models of

biomass productivity. None of the crop models reviewed in this paper explicitly uses this coupling.

Results of Applications of System Models for Water Stress Management

Coordination and evaluation of alternative combinations of resource inputs (water and nutrients), quantitative evaluation of the system response to management, and early predictions of outcomes of management actions are some of the many possible uses of agricultural system models (Stapleton, 1970). In general, agricultural system models are tools that help us synthesize and integrate knowledge from the biological, physical, chemical, biochemical, and biophysical processes in the system and study their responses to crop, soil, water, nutrient, and pesticide management. Such models can potentially have tremendous applications in research, education, and development of decision support tools for resource management in agriculture. In this direction, we made a critical review of literature to explore and record below a few examples of potential applications of the above five system models in plant water management research and extension.

APSIM

The cropping systems simulation model APSIM-N wheat was tested against detailed field measurements from a water stress experiment simulated by a rain-shelter at Lincoln, New Zealand (Fig. 1–3) (Asseng et al., 2004). The effects of different timing and duration of water deficit on crop growth and yield were reproduced with the model, where observed grain yields were reduced from 10 to 4 Mg ha^{-1} because of increased water deficit. However, the model underestimated
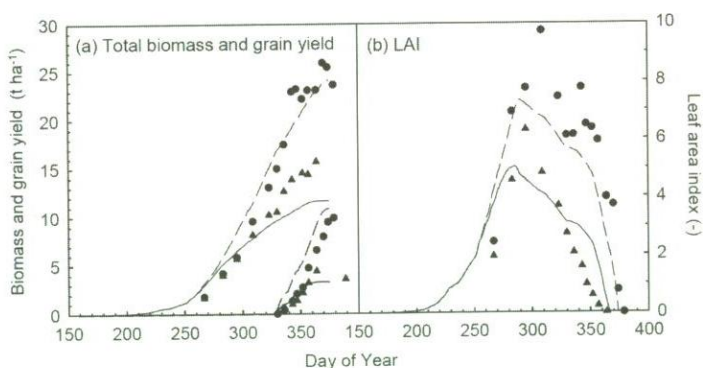

Fig. 1–3. APSIM simulated wheat growth and development in a rain-shelter experiment at Lincoln, New Zealand. Observed (symbols) and simulated (lines) for (a) total aboveground biomass and grain yield and (b) green leaf area index (LAI) for the well-watered treatment (●) and the most severe water limitation treatments (▲) (Asseng et al., 2004).

the late biomass accumulation in the severe water stress treatment (Fig. 1–3a). In soybean experiments from Western Australia, reduced growth and yields because of extreme terminal water deficit were also reproduced with the model, where measured yields fell below 0.5 Mg ha^{-1} (Robertson and Carberry, 1998).

CropSyst

Stöckle et al. (1994) tested the CropSyst model for yield response to water and nitrogen management in spring wheat using data from an experiment conducted at Logan, UT (Baiden, 1983). There were six water application rates ranging from 0 to 315 mm and five nitrogen application levels ranging from 0 to 228 kg N ha^{-1} for a total of 30 different managements. Predicted and measured grain yield and aboveground biomass compared quite satisfactorily (Fig. 1–4).

DSSAT-CSM

Ben Nouna et al. (2000) reported successful testing of the CERES-Maize model in a semiarid Mediterranean environment during a 2-yr period with the maize crop grown under three different soil-moisture conditions: full irrigation (IRR), moderate water stress (STR1), and severe stress (STR2). In well-watered plots, the model adequately simulated growth and yield (differences between simulated values and observations were less than 10%) (Table 1–1). However, under mild soil-water shortage, the model underestimated the leaf area index (LAI) (up to 26% for maximum LAI), above-ground biomass (up to 23%), and grain yield (up to 15%). Mismatches between observations and predictions increased with water
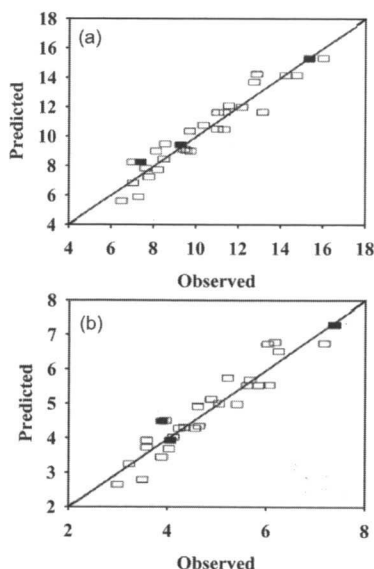

Fig. 1–4. CropSyst simulated and observed (a) spring wheat biomass and (b) spring wheat grain yield in response to water and nitrogen treatments at Logan, UT, in 1982. Dark symbols represent calibration points (Stöckle et al., 1994).

Table 1–1. Comparison between CERES-Maize simulated and observed data for each treatment and percent difference (Ben Nouna et al., 2000).

Variable	Units	IRR			STR1			STR2		
		Predicted	Observed	D (%)	Predicted	Observed	D (%)	Predicted	Observed	D (%)
1996										
Anthesis date	doy†	213	213	–	212	214	-0.94	212	218	-2.7
Maturity date	doy	262	262	–	270	270	–	270	270	–
Grain yield	kg ha⁻¹	8046	8676	-7.26	6339	6836	-7.27	4441	5030	-11.71
Kernel weight	g	0.2059	0.2400	-14.20	0.2276	0.2100	+8.38	0.2235	0.2000	+11.75
Grains m²	–	3908	3615	+8.11	2785	3255	-14.44	1987	2515	-20.66
Grains per ear	–	781.5	723	+8.09	556.93	651	-14.44	397.45	503	-20.99
Max. LAI	–	4.14	4.1	+0.97	2.6	3.52	-26.14	1.67	2.81	-40.57
Biomass	kg ha⁻¹	17,638	18,674	-5.55	12,429	16,134	-22.96	9266	13,099	-29.26
Seasonal ET	mm	498	498.17	0	415	425.86	-2.55	359	372.06	-3.51
1997										
Anthesis date	doy	213	213	–	213	214	-0.47	213	217	-1.8
Maturity date	doy	262	262	–	262	262	–	262	262	–
Grain yield	kg ha⁻¹				6100	7212	-15.42	3975	5180	-23.26
Kernel weight	g				0.1938	0.2100	-7.71	0.1561	0.2000	-21.95
Grains m²	–				3147	3434	-8.35	2547	2590	-1.66
Grains per ear	–				629.34	686	-8.26	509.33	518	-1.67
Max. LAI	–				2.95	3.47	-14.98	1.61	2.99	-46.15
Biomass	kg ha⁻¹				13,355	15,665	-14.74	8717	11,591	-24.80
Seasonal ET	mm				440	442.07	-0.47	313	338.9	-7.64

† Day of the year.

stress level (by up to 46, 29, and 23% for maximum LAI, biomass, and grain yield, respectively). These underestimations of LAI, biomass, and grain yield while predicting nearly correct ET are consistent with findings of Sau et al. (2004) that the use of the Priestley-Taylor function in the DSSAT-CSM models tend to predict too much ET (too much growth reduction) and that the extinction coefficient for partitioning EO to transpiration (EPO) is too high in CERES-Maize V3.5 used by Ben Nouna et al. (2000). As a result of work by Sau et al. (2004), the extinction coefficient (Kep) on LAI for partitioning EO to EPO for CERES Maize V4.0 was reduced from 1.00 to 0.68, which minimizes the overly high predicted ET rate during early season (30–60 d) and conserves water to later in the season, which would improve biomass and yield predictions. Sau et al. (2004) added an FAO56 ET option to the DSSAT-CSM models that improved predictions of fababean (*Vicia faba* L.) in their study and would also cause greater prediction of biomass and grain yield in the Ben Nouna study. The FAO56 ET option was shown to be better than the Priestley-Taylor option, also confirmed by Allen et al. (1998).

Nielsen et al. (2002) calibrated and tested the CROPGRO module in DSSAT v3.5 for simulations of soybean growth, yield, and water use under a range of water stress conditions normally encountered by dryland production systems in the Great Plains, USA. The model correctly predicted the evaportanspiration (ET), leaf area development, biomass, and grain yield (e.g., Fig. 1–5 and 1–6). Despite reasonable performance (Fig. 1–5 and 1–6), the tendency to simulate too high ET at low values of measured ET confirms the findings of Sau et al. (2004) that the extinction coefficient (Kep) was too high in CROPGRO V3.5 (Kep was decreased from 0.85 to 0.70 for V4.0 release) and that Priestley-Taylor tends to over predict ET slightly in cooler but relatively arid locations.

GLYCIM

Reddy et al. (1995) tested the model, which has been improved for enhanced simulations of the effect of water stress on several physiological processes in the soybean plant, with data collected on several cultivars grown in farmers' fields in the Mississippi Delta with various soil types, weather scenarios, and management conditions during 1991 through 1993. These data represent over 20 crop years with varying planting dates, maturity groups, row spacing, plant density per meter row, and management inputs. At the time of germination, plots were laid out for destructive and nondestructive sampling with four replications. Throughout the season, control practices were employed to avoid any significant weed, insect, or disease problems. Reasonable agreement between simulated and observed seasonal development of plant height and vegetative and reproductive
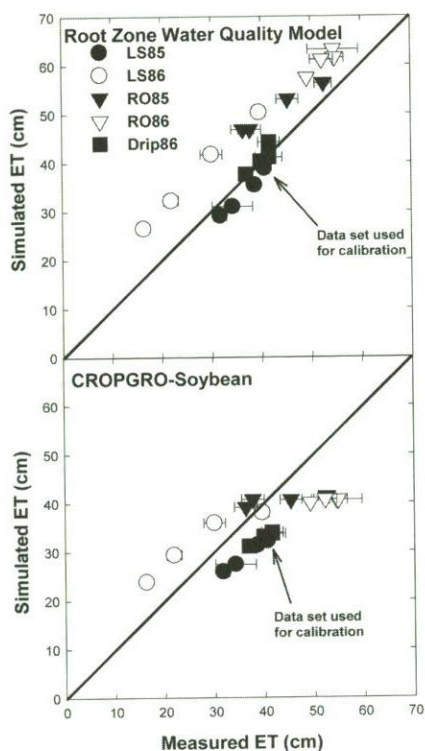
Fig. 1–5. Measured vs. simulated soybean evapotranspiration at Akron, CO. Bold diagonal line is 1:1 line. LS, line-source gradient irrigation experiment; RO, rainout shelter experiment; Drip, drip irrigation experiment (Nielsen et al., 2002).
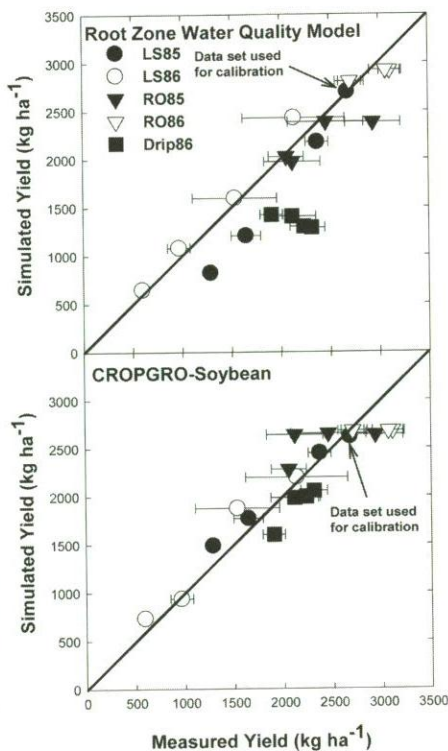
Fig. 1–6. Measured vs. simulated soybean yield at Akron, CO. Bold diagonal line is 1:1 line. LS, line-source gradient irrigation experiment; RO, rainout shelter experiment; Drip, drip irrigation experiment (Nielsen et al., 2002).

stages for the soybean cultivar DPL 415 grown in Sharkey silty clay soil in the Mississippi Delta was observed (Fig. 1–7).

GLYCIM was used to schedule irrigation in a study with soybean growers in the Mississippi Delta for a period of 8 yr (Timlin et al., 2002). The growers reported up to 25% increases in yields and 400% increase in irrigation efficiency that was attributed to the use of the model. The growers had been basing their irrigation estimates on visual inspection of the plants. GLYCIM simulations showed that water stress was already affecting yield by the time the growers began irrigating. Also, the growers were irrigating the cracked clay soils (Sharkey series) when they were too dry and had large cracks. When the soils were irrigated earlier, much less water was lost to deep drainage and irrigation efficiency increased.
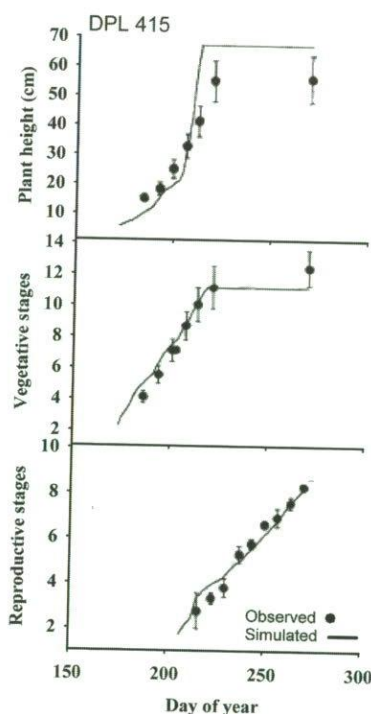
Fig. 1–7. Comparison of GLYCIM simulated and observed seasonal development of plant height and vegetative and reproductive stages for soybean cultivar DPL 415 grown in Sharkey silty clay soil in the Mississippi Delta. (Reddy et al., 1995).

RZWQM

Ma et al. (2003) evaluated the RZWQM for its ability to simulate the responses of maize growth and yield to various levels of water stress. Data sets collected in 1984, 1985, and 1986 in northeastern Colorado were used for the model evaluation. Three irrigation levels were imposed in 1984 and four levels in 1985 and 1986. Measurements included soil-water content in 1985, leaf area index (LAI) and aboveground biomass in 1984 and 1985, and maize yield and plant height in 1984, 1985, and 1986. The RZWQM was calibrated for the lowest (driest) irrigation treatment in 1985 and then used to predict soil water and agronomic attributes for other irrigation treatments in all 3 yr. Overall, the model responded well to irrigation treatments and weather conditions (Fig. 1–8). Prediction of plant height was adequate in 1985 and 1986. Although biomass was reasonably predicted in early and late growing seasons, it was over-predicted during the middle growing season in both 1984 and 1985. However, maximum LAI and plant height were over-predicted in 1984. Total soil-water storage was well predicted in 1985 and so was evapotranspiration (ET) during the crop growing season. Yield predictions were within 1 to 35% of measured values for all the 3 yr (Fig. 1–8). Even with a low prediction of yield in 1986, the model correctly simulated the relative increase of yield with irrigation amount.
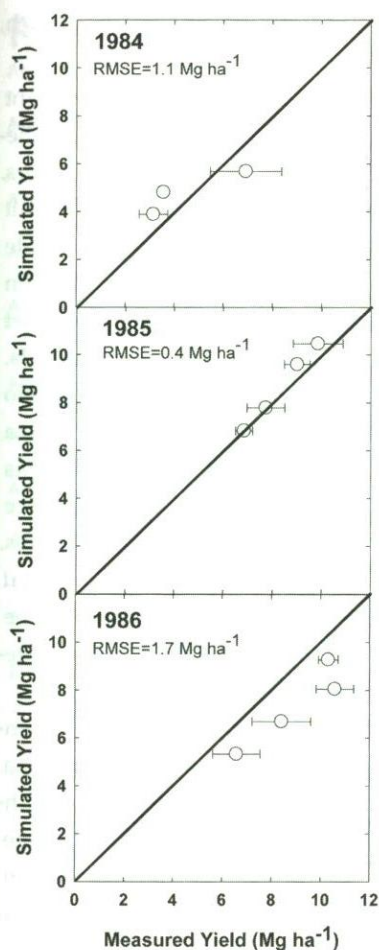
Fig. 1–8. Measured and RZWQM simulated corn yields in 1984, 1985, and 1986. Vertical bars represent one standard deviation around the mean values (Ma et al., 2003).

Conclusions

A model is generally built to represent the system in the simplest way possible, staying within the constraints of the objectives, user domain definition, resources, and time frame of the modeling endeavor. In this review article, first we presented a brief but critical overview of the current level of understanding of the plant physiological responses to soil-water deficit stress. Further, we made an attempt to explore and describe the various ways in which water stress quantification and interactions with various plant processes have been addressed in five (APSIM, CropSyst, DSSAT-CSM, GLYCIM, and RZWQM) major agricultural system models, for a general audience. We concluded the article with examples, as available in published journal articles, of testing and applications of these models

for simulation of field experiments in which water stress effects on plant growth, development, and yield were explored.

Studies in the past showed that, in general, water stress affects the plant phasic developmental rates, leaf initiation and expansion growth, photosynthesis, carbon allocation and partitioning, and root length and density in soil layers. However, these responses and interactions vary among crops, making it difficult in the development of generic plant growth modules for simulations of multiple species. A better understanding of the water stress effects on biomass allocation and partitioning in specific crop species and cultivars is needed because that would help in better representation of these processes in respective crop models.

With the exception of GLYCIM, all the above models make use of the ratio of potential to actual transpiration for quantifying water stress. GLYCIM uses a more mechanistic approach to modeling water stress affects on photosynthesis and expansion growth. There were no explicit simulations of leaf energy balance and temperature simulations in quantifying transpiration in any of the models. There is a need for enhanced mechanical simulation and coupling of stomatal conductance, photosynthesis, respiration, and energy balance processes in the models reviewed. A brief review of the models reported in the literature that integrate and couple the above processes were presented.

Review of literature showed that so far, use of the models in water management research were largely confined to only testing the model against data collected from specific water stress treatments in field experiments. Notwithstanding the simplicity or complexity or the level of details incorporated in the five models reviewed, once calibrated they were able to simulate the experimental ET, biomass, and grain yield in field research equally well with reasonable accuracy. However, the data do not show accuracy in a model's individual processes. Compelling applications of the models in crop water management research for improving water-use efficiency in agriculture were not widely attempted. See Timlin et al. (2002) for an example with GLYCIM and Gertis and Whisler (1998) for an example with the cotton model GOSSYM. It is felt that, for putting models to better use in research and planning, there is an urgent need for integrating models in field research from the very planning and design stage to extension of outcomes beyond the temporal and spatial scales of the experiment. This would allow modelers to work synergistically with experimentalists to generate soil–water–plant data for validation and improvement of the models for applications for better water-use efficiency in cropping systems.

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